Distribution of attacks and egg galleries by the spruce beetle around the bole of windthrown trees

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ABSTRACT

The distribution of attack density and egg gallery length by the spruce beetle around the bole of windthrown spruce trees was investigated in central British Columbia. In windthrown trees that are oriented north–south or east–west, the circular distributions of both attack density and egg gallery length were significantly different from the uniform distribution. The mean directions for the center of mass of the distributions suggest an evolved preference by the spruce beetle for establishing broods relative to habitat quality. The preferred habitats for brood establishment were the shaded bottoms and lower sides of windthrown trees. This finding is consistent with the hypothesis that attack preference is a function of solar insulation during the attack period.

Key Words: Spruce beetle, attacks, circular distribution, survival, sampling

INTRODUCTION

The spruce beetle, *Dendroctonus rufipennis* (Kirby) (Coleoptera: Curculionidae, Scolytinae), is native to spruce (*Picea sp.*) forests of North America (Bright 1976). Endemic spruce beetle populations breed in fresh windthrown trees, logging residue, injured, diseased or decadent trees. Spruce windthrow is common in mature spruce forests and is the preferred host material of the spruce beetle even during outbreaks (Schmid 1981).

Windthrown trees, especially those that are scattered in stand interiors provide superior breeding habitat for the spruce beetle over standing trees likely because of attributes such as snow cover that protects the broods from extremely cold temperatures and from predation by woodpeckers. Windthrow occurs more frequently in the larger-diameter classes and may also offer better nutritional conditions for brood survival compared to standing trees with low vigour.

Dyer and Taylor (1971) reported higher brood survival by the spruce beetle on the bottom of windthrown trees compared to the upper sides and Schmid (1981) found differences in both attack density and brood densities among the tops, sides and bottoms of windthrown trees. My objective was to test the null hypothesis that the circular distribution of attack densities and egg gallery lengths/m^2 around the bole circumference of spruce windthrow is uniform and independent of the direction of fall. I have quantified the circular distributions and provided an explanation in terms of the adaptive and practical significance of the results.

MATERIALS AND METHODS

The study site was located approximately 75 km southeast of Prince George, British Columbia, in the Naver Creek watershed (53°24' N; 122°20' W), at an elevation range of 900 m to 1400 m. The stands comprised mature (> 150 years) hybrid white spruce (*P. glauca* x *P. engelmanni* hybrid population) and subalpine fir [*Abies lasiocarpa* (Hook) Nutt.], with an average stand density of 171 stems per hectare

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greater than 20 cm diameter at breast height (dbh). Spruce dominated the overstorey, making up 73.1 % of the stems greater than 20 cm dbh, with an average diameter at 1.3 m (dbh) of 50.5 cm. A few mature Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco], lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.), white birch (*Betula papyrifera* Marsh.), and aspen (*Populus tremuloides* Michx.) were scattered throughout the study areas.

The windthrown trees used in the study were located in stand interiors and were attacked by spruce beetle during the spring of 1974. The following spring, bolts cut from six and five separate windthrown trees, oriented north–south (N-S) and east–west (E-W), respectively, were sampled to determine the circular distribution of spruce beetle attacks and egg gallery lengths around the bole. Prior to cutting, the top of each bolt was determined and marked as the midpoint between vertical posts positioned next to the bole on opposite sides.

From each selected N-S tree, one bolt averaging 42.1 cm in length (range: 29.6 cm to 51.8 cm) was cut from each of the bottom, middle and top third of the infested bole. The average diameter of the bolts was 33.8 cm (range: 21.3 cm to 46.6 cm). From the selected E-W trees, 13 bolts were cut, one to four bolts per tree. The average length and average diameter of the bolts were 41.4 cm (range: 28.9 cm to 56.1 cm) and 32.6 cm (range: 26.8 cm to 54.8 cm), respectively. In the laboratory, each end of each bolt circumference was divided into nine equal strips, each strip representing a 40° angular interval. On bolts cut from N-S windthrow, the first such interval was designated as being located directly west of the top of the bolt. On bolts cut from E-W windthrow, the first 40° angular interval was designated as being located directly north of the top of the bolt. Continuing from the top around the circumference of the bolt, each strip was designated by the midpoint of the respective angular interval; e.g., 20°, 60°, ..., 340°.

All bark was carefully removed from each strip, and the following information was recorded:

- strip length and width;
- number of egg gallery entrances (attacks), and;
- length of exposed egg galleries.

Egg gallery length in a bark strip was defined as the sum of the lengths of all complete egg galleries and the lengths of all partial egg galleries. The number of attacks and total egg gallery lengths were converted to numbers per square meter prior to analysis by dividing respective totals by the strip bark area. In what follows, egg gallery length/m^2 is referred to as egg gallery length.

For bolts cut from N-S windthrow, variation in attack density and egg gallery length by tree and bolt position were analysed by analysis of variance in a randomized complete block design with windthrown trees as blocks. For bolts cut from E-W windthrow, variation in attack density and egg gallery length by windthrow was analysed by analysis of variance in a completely randomized design. The relationship between densities of attack and egg gallery length was analysed by linear regression. For bolts cut from N-S windthrow, the empirical circular distributions by bolt position and of the total number of attacks were compared by chi-square test, as were the overall empirical circular distributions of the total number of attacks by windthrow orientation (Batschelet 1965).

The statistics for the empirical circular distributions of attack density and egg gallery length by windthrow orientation were calculated as in Batchelet (1965). Based on the observed angular distribution of attacks and egg gallery lengths, the mean direction (α_m) was calculated as follows:

[1a] $\alpha_m = \arctan\{[(1/n)\ \Sigma^n \sin(\alpha_i)]/[(1/n)\ \Sigma^n \cos(\alpha_i)]\}$, if $(1/n)\ \Sigma^n \cos(\alpha_i) > 0$.

[1b] $\alpha_m = 180° + \arctan\{[(1/n)\ \Sigma^n \sin(\alpha_i)]/[(1/n)\ \Sigma^n \cos(\alpha_i)]\}$, if $(1/n)\ \Sigma^n \cos(\alpha_i) \leq 0$,

where α_i = the angle corresponding to the midpoint of angle class i. The length of the mean vector (r), dispersion about the mean direction in radians (s) and skewness (g) were calculated as given in equation 2, 3 and 4, respectively:

[2] $r = (x^2 + y^2)^{0.5}/n$; $x = \Sigma^n \cos(\alpha_i)$, $y = \Sigma^n \sin(\alpha_i)$, n = sample size.

[3] $s = [2(1-r)]^{0.5}$

[4] $g = r_2 (\sin (2\alpha_m - \alpha_{2m})$, α_{2m} is calculated as in equations [1a] and [1b] and r_2 is calculated as in equation [2] but by doubling each angle α_i

The Rayleigh test (z; Batschelet 1965) was used to test the null hypothesis that the distribution of the direction of fall of windthrown trees was uniform (equation 5).

[5] $z = nr^2$

RESULTS

In N-S windthrow, there was significant variation among windthrow in attack density, but not in egg gallery length or in either of these variables among bolt positions within trees (Table 1). The mean attack density and egg gallery length was 18.3/m^2 and 250.1cm/m^2, respectively. In E-W windthrow, there was no significant variation among trees in attack density or egg gallery length (Table 1). The mean attack density and egg gallery length was 20.9/m^2 and 278.3 cm/m^2, respectively.

The relationship between egg gallery length/m^2 (Y) and attack density/m^2 (X) was linear for both windthrow orientations (Figure 1). The equation for the combined data is given in equation 6.

[6] Y = 21.47 + 12.93 X, n = 135, r = 0.839, s.e. = 145.82

The intercept of [6] was not significantly different from zero (t =1.285, p = 0.20). The estimated average egg gallery length per attack based on the zero intercept regression of Y on X (equation 7) was 13.55 cm.

[7] Y = 13.55 X

Even though there was a strong linear relationship between egg gallery length and attack density, mean egg gallery length per attack tended to be higher in those orientation angle classes that corresponded with the highest mean attack densities (Figure 2).

In N-S windthrow, there was no significant difference in the circular distributions by bolt position of attack totals per strip ($\chi^2_{(12df)} = 12.83$, p = 0.37). Based on this finding, and the observation of no difference in either attack or egg gallery length among bolt positions, and the highly significant correlation among attack density and egg gallery length, analysis of the circular distributions of attack density and egg gallery length was done on data combined over bolt position.

The circular distributions of attack (a) and egg gallery length (e) differed significantly from uniform distributions in bolts cut from windthrow oriented either N-S or E-W (Table 2). The length of the mean vector and the dispersion about the mean direction for each of the variables (a) and (e) were nearly the same magnitude in both windthrow orientations. The mean angles were nearly identical for attack density and egg gallery length within, but not between, the two orientations (Table 2). In N-S windthrow, the mean angles for both variables were greater then the respective means in E-W windthrow. The distribution of egg gallery length was more skewed than that for attack density, especially in N-S windthrow (Table 2).

There was no difference in the empirical circular distributions of attacks per bark strip in windthrow of the two orientations (Table 3). This result is explained by the nerly identical mean vectors and dispersions of attack density in windthrow of the two orientations (Table 2). Because attack density and egg gallery length were highly correlated, the distribution of the latter was largely determined by that of the former. In windthrow, of both orientations, both attack density and egg gallery length were highest on the bottom quadrants of the trees. (Figures 3 and 4). The respective means corresponded with the angular intervals 120° to 160°, 240° to 280° (north–south) and 80° to 120°, 200° to 240° (east–west).

Table 1.
F-statistics and associated probability levels for variation among windthrown spruce trees and among positions in trees of attack density and egg gallery length for windthrow oriented north–south and for variation among windthrow oriented east–west.

Source of variation	Attacks/m^2	Egg gallery length/m^2
	Windthrown trees oriented north–south	
Trees	$F_{4,8\ df} = 4.324$, $p \leq 0.037$	$F_{4,8\ df} = 1.575$, $p \leq 0.270$
Position	$F_{2,8\ df} = 2.139$, $p \leq 0.180$	$F_{2,8\ df} = 0.126$, $p \leq 0.883$
	Windthrown trees oriented east–west	
Trees	$F_{5,7\ df} = 0.609$, $p \leq 0.697$	$F_{5,7\ df} = 2.688$, $p \leq 0.115$

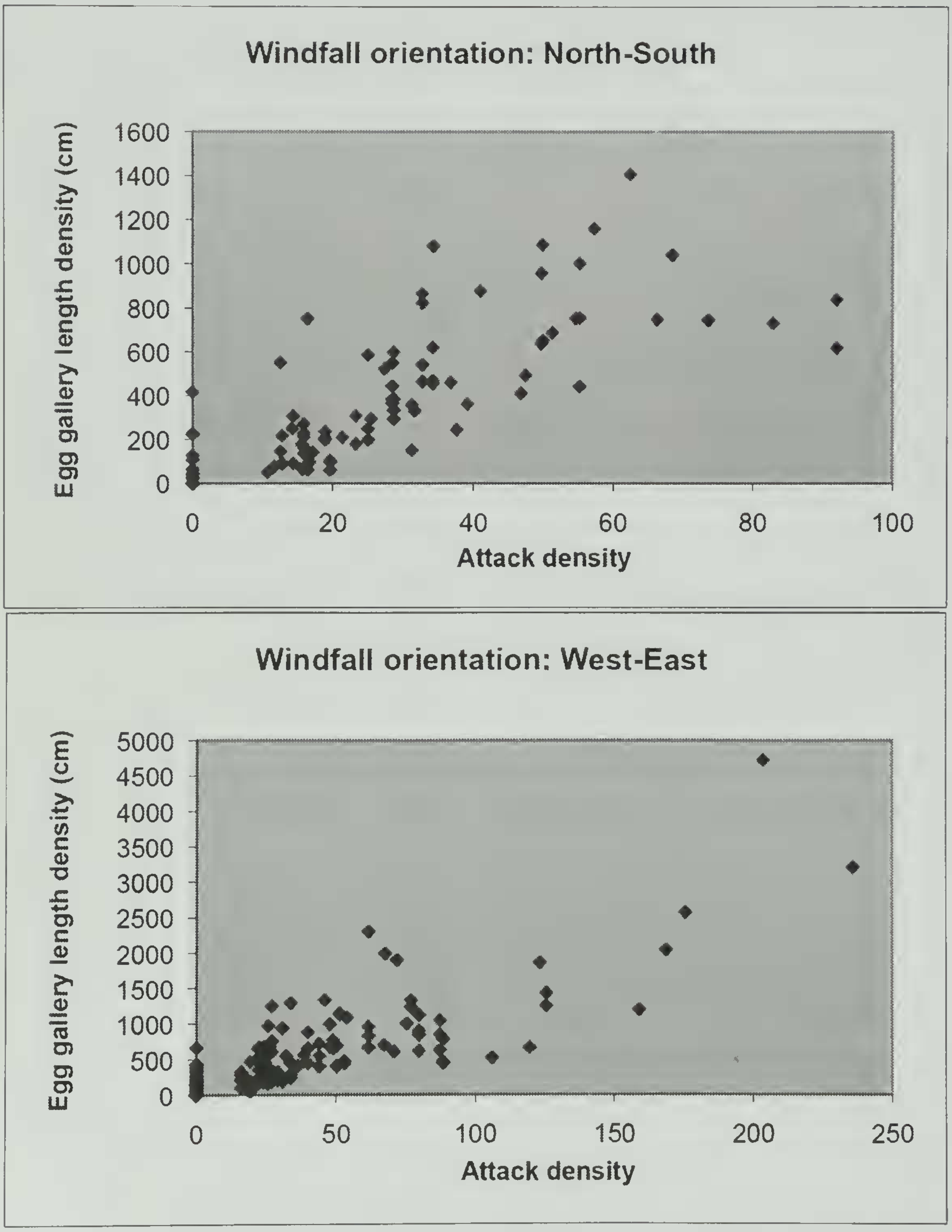

Figure 1. Relationship between egg gallery length (cm)/m^2 and attack density/m^2 by the spruce beetle in spruce windthrow oriented in two directions. Pooled data from all orientation angle classes.

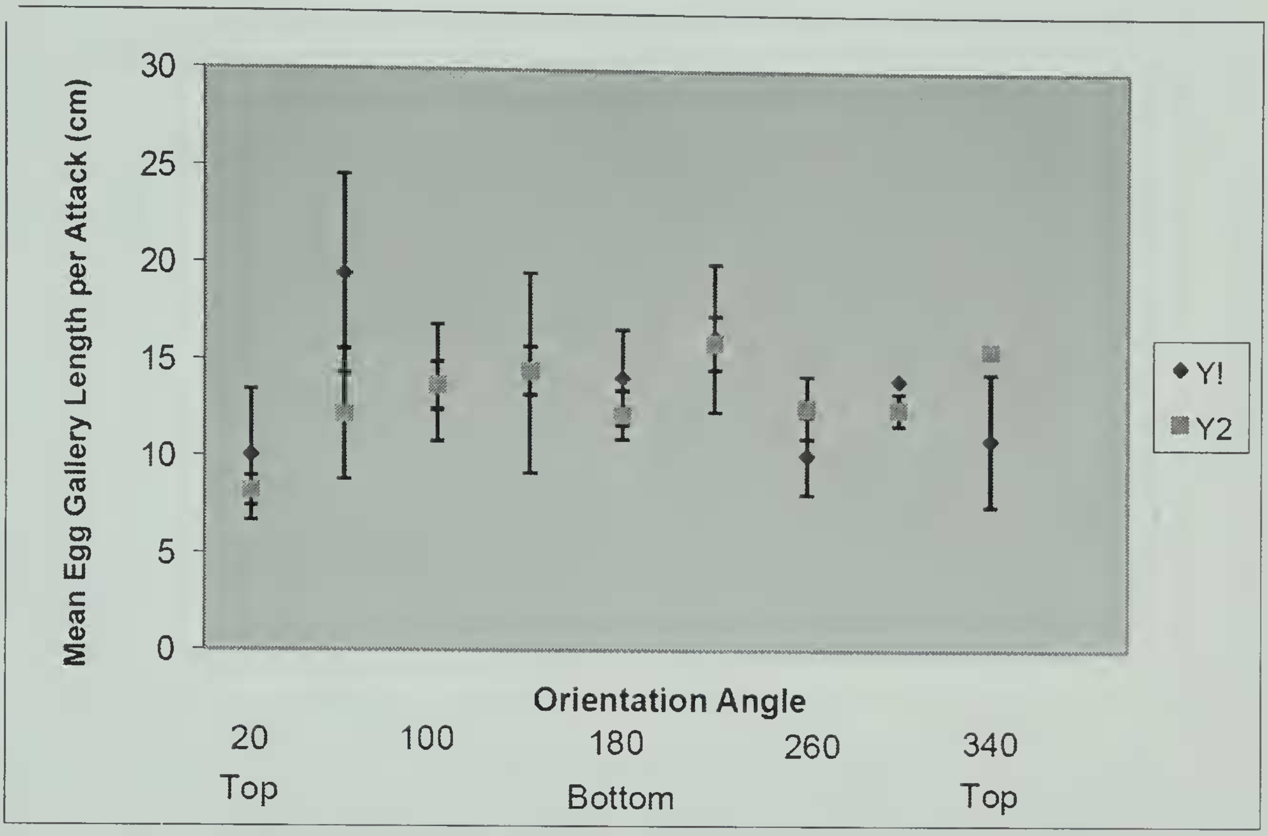

Figure 2. Mean egg gallery length per attack (±1SD) by the spruce beetle in windthrow oriented north–south (Y2) and east–west (Y1) around the circumference of the bole.

Table 2.
Statistics for the empirical distributions of attack density and egg gallery length around the bole in spruce windthrow oriented in two directions.

Statistic[1]	Direction of fall			
	North–South		East–West	
	Attacks/m^2	Egg gallery (cm)/m^2	Attacks/m^2	Egg gallery (cm)/m^2
Mean direction (α_m)	184.9°	182.1°	167.3°	166.4°
Mean vector (r)	0.307	0.350	0.284	0.317
Dispersion (s)	67.5°	65.3°	68.6°	67.0°
Skewness (g)	0.034	0.150	0.085	0.114
$Z=nr^2$	15.268**	27.685**	8.720**	13.767**

[1] See equations 1 to 5 in Methods
** Significant at $p \leq 0.01$

DISCUSSION

Mean attack density, egg gallery length, and mean egg gallery length per attack found in this study are typical for endemic spruce beetle populations in spruce windthrow in central British Columbia. Over a five-year period in the Naver Forest, the yearly mean attack density by spruce beetle in windthrow ranged from 14.7/m^2 to 51.7/m^2, and the corresponding range in egg gallery length was 120cm/m^2 to 670cm/m^2 (Safranyik and Linton 1999). The mean egg gallery length per attack found in this study (13.55 cm) was well within the range reported by Safranyik and Linton (1999; 8.2 cm to 19.8 cm) and close to the average egg gallery length in spruce bolts (12.7 cm; Safranyik and Linton 1983) and trees (13.0 cm; Wood 1982). The lack of significant variation by bolt position in attack density and egg gallery length was surprising, con-

Table 3.
Chi-square test of the empirical distributions around the bole of attacks per bark strip by the spruce beetle in spruce windthrow oriented in two directions.

Angle class mid-point	Observed			Expected	
	North–South	East–West	Sum	North–South	East–West
20 (top)	7	8	15	9.0	6.0
60	11	8	19	11.4	7.6
100	13	16	29	17.4	11.6
140	30	17	47	28.2	18.8
180 (bottom)	28	18	46	27.6	18.4
220	22	19	41	24.6	16.4
260	29	10	39	23.4	15.6
300	11	9	20	12.0	8.0
340 (top)	11	13	14	8.4	5.6
Sum	162	108	270	162	108

$\chi^2_{(8df)} = 10.54$, p=0.23

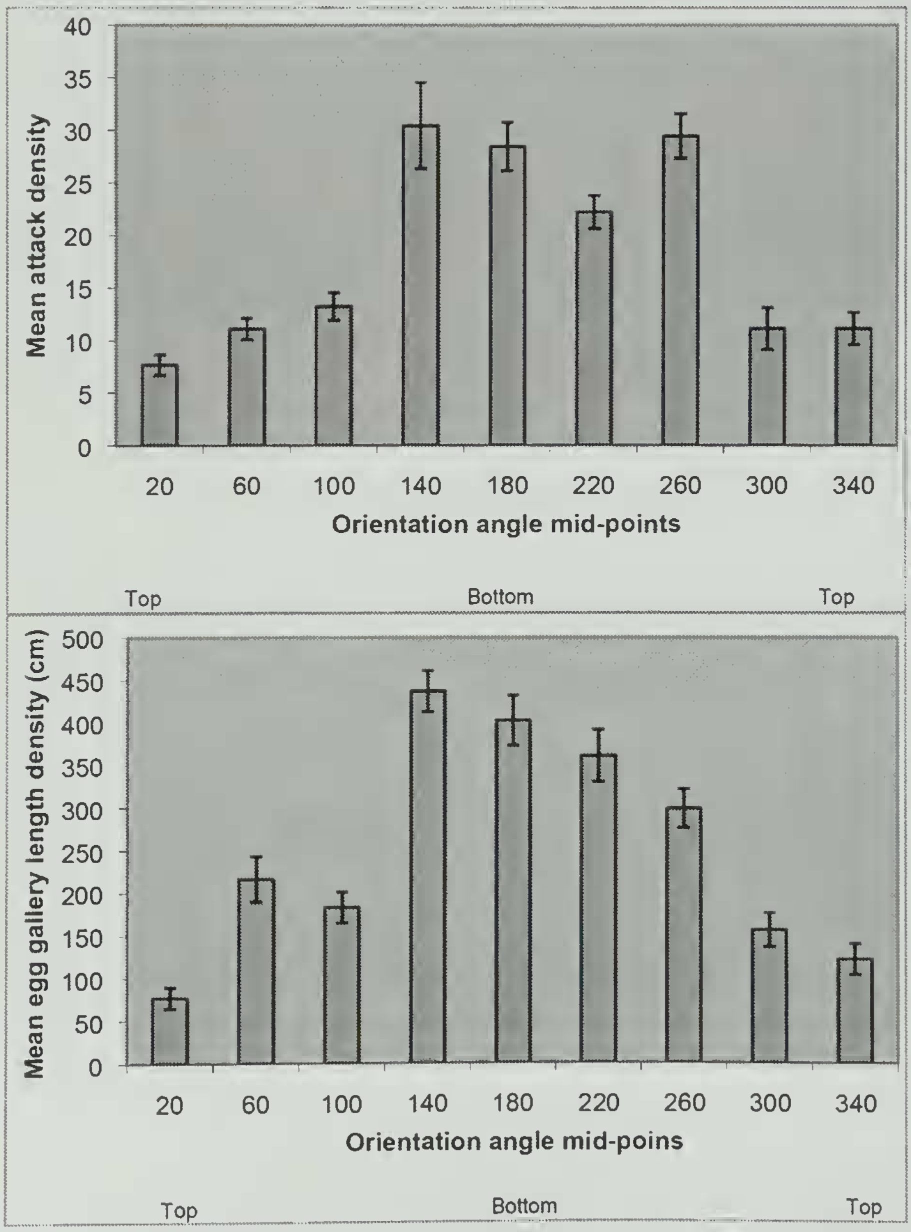

Figure 3. Empirical circular distribution of mean attack density/m2 (±1SE) and egg gallery length/m2 (±1SE) by the spruce beetle on spruce windthrow oriented north–south.

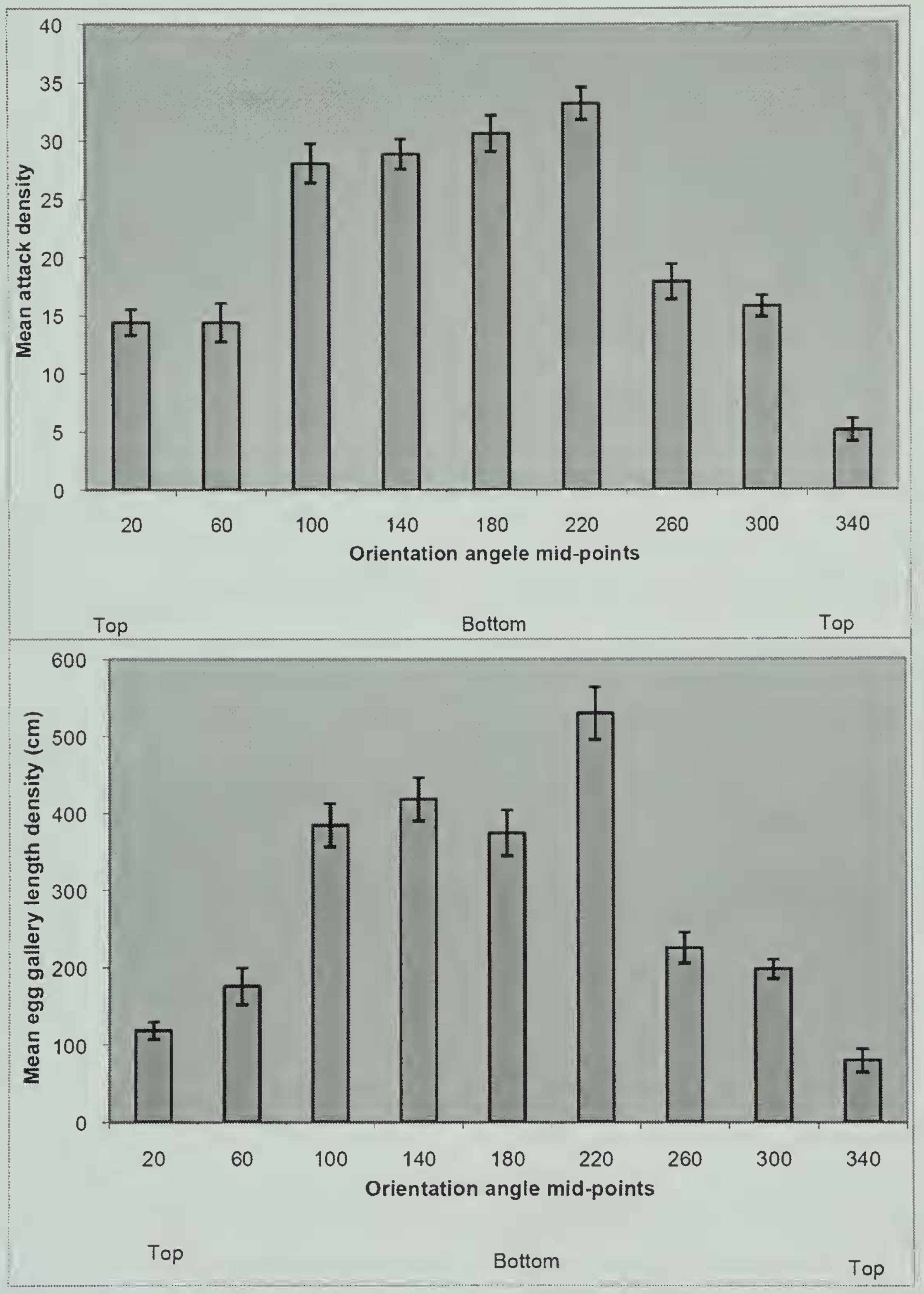

Figure 4. Empirical circular distribution of mean attack density/m^2 (±1SE) and egg gallery length/m^2 (±1SE) by the spruce beetle on spruce windthrow oriented east–west.

sidering changes along the bole in host variables such as diameter, bark thickness branch size and density, and the humped distribution of attacks on height above ground (Safranyik and Linton 1987).

Even though there was a strong linear relationship between attack density and egg gallery length, mean egg gallery length per attack tended to be higher in the orientation-angle class that had the highest attack densities (Figure 2). This suggests that, in addition to attack density, the position of an attack on the bolt circumference affected egg gallery length per attack. This effect explains, in part, the relatively greater skewness of the empirical circular distributions of egg gallery length compared to the attack density (Table 2; Figures 3 and 4).

The results reported in this paper regarding the distribution of attacks around the bole by the spruce beetle in windfall confirm earlier results. Safranyik and Linton

(1987; 1988) reported higher attack densities by the spruce beetle on the north aspects of trees, near the duff, and the shaded (northeast and southeast) aspects of stumps. Schmid (1981) reported that, in windthrow, attack and brood densities were the highest on the bottom, lowest on the top, and intermediate at the sides of the bole. Moreover, Safranyik and Vithayashai (1971) found a significantly non-uniform circumferential distribution of attacks by the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) around the bole of lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelmann) with highest attack density corresponding to the shadiest aspect of the bole during the time of peak daily attack period.

The highly significant mean vectors for the circular distribution of attack and egg gallery length in windthrown trees of both orientations indicate an evolved preference for brood establishment based on habitat quality. In both windfall orientations, there was a strong preference by beetles to establish attacks on the bottom of the bole, as indicated by the direction of the mean vector. In N-S and E-W windthrow, the "center of mass" of attacks was located 5° east and 13° north of bottom center of the bole, respectively. Due to the low density of the overstory trees in this study (mean distance among neighbouring trees =7.6 m), most windthrow received only light to moderate shading, resulting in differences in insulation on various aspects of the bole. In N-S and E-W windthrow, excepting the bottom of the bole, respectively the east and north sides would have received the least insulation during peak daily attacks.

In mature spruce forests, most of the endemic windthrow is comprised of larger-diameter trees (Stathers et al. 1994). Windthrown trees have no resistance to attack, and often provide a large and thermally stable phloem resource for exploitation, especially at the bottom and sides of the bole. Frequently, some roots of windthrown trees are not torn from the ground and remain functional for some time. This also can contribute to maintaining phloem quality, especially on the undersides of windthrown trees. As described in the Introduction, spruce beetles in windthrown trees are protected by snow cover during winter from extremely low temperatures as well as from predation by woodpeckers. All of these characteristics make spruce windthrow in general, and especially the bottom and sides, preferred habitat for spruce beetle. This preference apparently evolved even though the rates of brood development in shadier sides of windthrow are reduced, resulting in an extended life cycle in the preponderance of the brood in most years. Hence, it appears that the evolution of this preference is the result of a trade off between development rates and survival.

Based on studies of mountain pine beetle behaviour in relation to heat and light conditions, Shepherd (1965) hypothesized that both high heat and high light intensity stimulate flight. Therefore attacking beetles tend to seek the shadier aspects of the bole. This hypothesis is consistent with the nature of the circular distribution of spruce beetle attacks in windthrow, as well as published information cited earlier regarding the distribution of attacks by this species in trees and stumps, as well as attack and brood densities in windthrow.

The results presented here have implications for sampling spruce beetle populations in windthrow to determine population density, brood survival and the relative sizes of the attacking (parent) and emerging (offspring) population. These results indicate that reliable estimates of mean attack density may be obtained by taking samples along the sides of the bole. However, as the distribution around the bole of brood survival is affected by a number of factors in addition to attack density (including habitat quality, competition for food and space, and predation), the location around the bole of mean brood survival may be different from that of attack density and egg gallery length.

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